

Effects of water stress on total biomass, tuber yield, harvest index and water use efficiency in Jerusalem artichoke



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ABSTRACT

The objectives of this study were to determine the effects of drought on tuber yield, total biomass, harvest index, water use efficiency of tuber yield (WUE_t) and water use efficiency of biomass (WUE_b), and to evaluate the differential responses of Jerusalem artichoke (JA) varieties under drought stress. The 3 × 5 factorial combinations of three water regimes (Field capacity (FC), 50% available soil water (50%AW) and 25%AW), and five JA varieties (JA 60, JA 125, JA 5, JA 89 and HEL 65) were arranged in a randomized complete block design with four replications for two years. Data were recorded for tuber dry weight, total biomass, harvest index, WUE_t and WUE_b at harvest. Drought reduced tuber dry weight, total biomass, harvest index, WUE_t and WUE_b, and reductions were more severe under the severe drought stress of 25%AW. Varieties were significantly different for all traits under drought and well-watered conditions. The JA varieties were classified into three groups. The first category was comprised of the JA 5 variety with high tuber yield potential and low drought tolerance, the second category consisted of JA 60 and JA 125 varieties with low tuber yield potential and high drought tolerance, and the third group included JA 89 and HEL 65 varieties with low tuber yield potential and low drought tolerance. The multiple regression analysis showed that tuber yield, total biomass and harvest index at 50%AW and 25%AW depended largely on the reductions of tuber yield, total biomass and harvest index under drought. Therefore, the results of this study recommend that the selection of JA genotypes with low reduction in yield under drought stress could be a criterion in drought resistance breeding programs for development of JA varieties with high tuber yield under drought stress. JA with drought tolerance in this study means high tuber yield under drought conditions. JA 5 had high yield and WUE_t across water regimes and could be used as parental source for drought tolerance breeding programs in further research.

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1. Introduction

Jerusalem artichoke (*Helianthus tuberosus* L.) is an important crop native to North America (Kays and Nottingham, 2008). Inulin containing tubers of Jerusalem artichoke with anti-cancer and immune enhancing properties can be consumed directly either as a vegetable or processed food to make several value-added products that are beneficial to health such as pharmaceutical products, food additive (Barclay et al., 2010) and feed additive (Sritiawthai

et al., 2013). It is also used as an energy crop for bioethanol production (Sachs et al., 1981). As gasoline price have increased, the crop has received more attention for use as raw material for biofuel production (Li et al., 2013; Kim et al., 2013).

Temperature increase in certain seasons around the world is the result of global warming leading to increased rates of water evaporation and thus surface drying, thereby increasing intensity and duration of drought (Trenberth, 2011). Drought is increasingly an important factor affecting crop production worldwide, and it also reduces tuber yield of Jerusalem artichoke (Conde et al., 1991; Losavio et al., 1997; Schittenhelm, 1999; Monti et al., 2005; Liu et al., 2012; Ruttanaprasert et al., 2014). Although effective irrigation scheduling may help in water saving for an irrigated crop in the short-term, breeding and selection of varieties that are more

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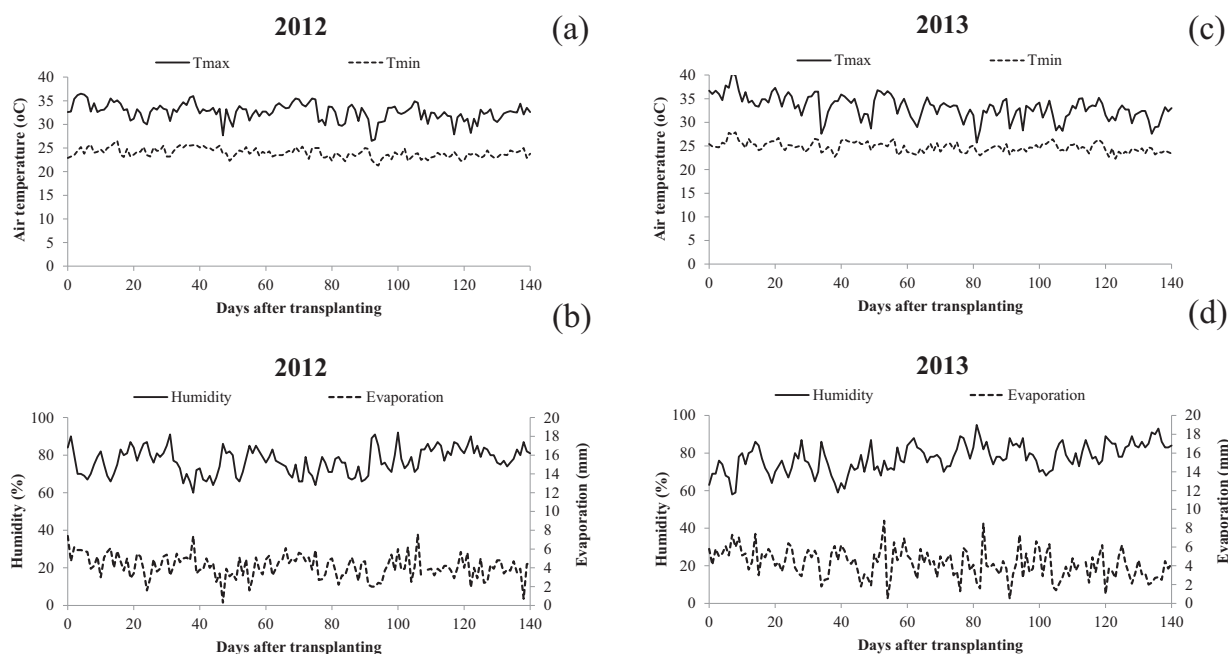


Fig. 1. Maximum temperature (T_{\max}), minimum air temperature (T_{\min}) ($^{\circ}\text{C}$), evaporation (mm) and humidity (%) in 2012 (a), (b) and 2013 (c), (d).

tolerant to drought should be the best long-term solution to the problem.

Effects of drought stress on tuber dry weight, biomass (Conde et al., 1991; Losavio et al., 1997; Schittenhelm, 1999; Monti et al., 2005; Liu et al., 2012; Ruttanaprasert et al., 2014) harvest index (Conde et al., 1991; Ruttanaprasert et al., 2015) and water use efficiency (Conde et al., 1991; Janket et al., 2013) of Jerusalem artichoke has been reported in several studies. In temperate regions, drought stress reduced Jerusalem artichoke tuber yield by 20% (Conde et al., 1991; Losavio et al., 1997) but increased water use efficiency by 7–35% and harvest index by 21% (Conde et al., 1991). In potato, terminal drought slightly reduced harvest index by 17% (Schafleitner et al., 2007). In tropical regions, drought stress with heat stress can cause tuber yield loss of 29% and biomass loss of 53%, however, some Jerusalem artichoke varieties can sustain yield to some extent under drought (Ruttanaprasert et al., 2014). Meanwhile, mild water stress caused 7.1% and 9.6% reductions in water use efficiency of biomass and tubers, respectively, but severe drought stress caused slight increases in water use efficiency of biomass (4.2%) and tubers (5.4%) (Janket et al., 2013). Drought also increased water use efficiency in cassava (Olanrewaju et al., 2009). Genotypic variations in tuber dry weight, biomass (without root mass) (Ruttanaprasert et al., 2014), harvest index (Ruttanaprasert et al., 2015) and water use efficiency (Janket et al., 2013) were found and used as selection criterion for Jerusalem artichoke productivity under drought stress.

The physiological basis for achieving higher yields under drought stress might indicate or show an underlying mechanism from where improved strategies could be developed to enhance the effectiveness and progress in breeding programs for drought resistance in Jerusalem artichoke. In one of the recently conducted studies, drought resistant varieties had higher tuber dry weight and biomass compared to drought-sensitive varieties (Ruttanaprasert et al., 2014). Higher crop productivity under drought stress of resistant varieties could be due to their ability to produce higher yield under well-watered conditions, i.e. higher productivity potential, or its ability to maintain high production, i.e. less yield reduction under drought stress (Pimratch et al., 2008). However, the relative

contributions of these two attributes to high crop yield of Jerusalem artichoke under drought conditions of resistant varieties have not been studied.

Therefore, the objectives of this study were to determine the effects of drought on tuber yield, total biomass, harvest index, water use efficiency of tuber (WUEt) and water use efficiency of biomass (WUEb), and to evaluate the differential responses of Jerusalem artichoke varieties under drought stress.

2. Materials and methods

2.1. Experimental design and treatments

A 3×5 factorial experiment was conducted for two years (May–September in 2012 and May–September in 2013) in the greenhouse and all the 15 treatments were replicated 4 times and arranged in a randomized complete block design (RCBD) at the Field Crop Research Station of Khon Kaen University located in Khon Kaen province, Thailand ($16^{\circ}28'N$, $102^{\circ}48'E$, 200 m above mean sea level). There were 5 pots in each experimental unit with one plant in each pot. Three water regimes (defined as field capacity (FC), 50% available soil water (50%AW) and 25% available soil water (25%AW)) were assigned in factor A, and five varieties of Jerusalem artichoke (JA 60, JA 125, JA 5, JA 89 and HEL 65) were assigned in factor B. Five Jerusalem artichoke varieties with different drought tolerance levels based on tuber yield under drought stress were selected (Ruttanaprasert et al., 2014). JA 60 and JA 125 had low tuber yield, JA 5 gave intermediate tuber yield, and JA 89 and HEL 65 gave highest tuber yield under drought stress (Ruttanaprasert et al., 2014).

2.2. Pots and plant preparation

Prior to planting, 20 kg of dry soil was loaded into 300 plastic pots with a diameter of 35 cm and height of 25 cm. The soil was equally divided into two layers to create uniform bulk density (of 1.61 g cm^{-3}) in each pot. The pots were first filled with 10 kg of dry soil taken from a depth of 10 cm below the soil surface to create

the first soil layer in the pots and perforated plastic tubes were installed in the middle of this layer to provide irrigation water to pots to maintain the required soil moisture contents in the pots. To create the second soil layer, the pots were further filled with the remaining 10 kg dry soil and soil was tapped to bring the surface of soil 5 cm below the top of the containers and another set of perforated plastic tubes was installed at 2.5 cm below the soil surface to supply irrigation water to this soil layer. The tubers were cut into small pieces with 2 or 3 buds per piece and soaked in a solution of carboxamide (10 g in 20 L of water) for 40 min. The tuber pieces were pre-sprouted in burnt rice husk mixed with trichoderma (3:1) under ambient conditions for 4–7 days. These sprouted tubers were transferred to germinating plug trays with mixed medium containing burnt rice husk, *Trichoderma* and soil (3:2:2) for 7 days for complete sprouting. *Trichoderma* was applied to each hill base. The healthy and uniform seedlings with 3–4 leaves were then ready for transplanting and one plant was transplanted in one pot as the experimental design criteria. The carboxamide and *Trichoderma* were used to control the stem rot diseases caused by *Sclerotium rolfsii* (Sennoi et al., 2013).

Manual weeding was done every day after transplanting (DAT) and mixed fertilizer of N–P₂O₅–K₂O (15–15–15) at the rate of 2 g pot⁻¹ (or 156.25 kg ha⁻¹) was applied at 15 DAT. Pests and diseases were controlled by application of wood vinegar for two times at weekly intervals (5 ml in 1 L of water) until harvest.

2.3. Water management

The water supplied to the pots was divided into two fractions. The first fraction was applied to the soil surface and the second fraction was applied through the tube installed at 10 cm below the soil surface. Prior to planting, water was supplied to all the pots to bring the soil moisture contents to field capacity level (20.5%) and the soil moisture was maintained at field capacity level until 10 DAT for uniform plant establishment. The irrigation treatments were initiated after 10 DAT. Soil water regimes were maintained uniformly at field capacity from transplanting until harvest in the well-watered treatment, and allowed to gradually reduce until they reached pre-determined levels at 13.9% for 50%AW and at 10.6% for 25%AW treatments at 14 DAT and 18 DAT, respectively. For each treatment, soil moisture content was maintained uniformly with no higher than 1% variance.

Irrigation water was added to the pots based on crop water requirement and to maintain the specified soil moisture levels as per the experimental treatments. The water supplied to individual pot was equal to the daily evapotranspiration rates of the crop (sum of water used by the crop and soil surface evaporation). The amount of needed irrigation water was calculated following the methods described by Doorenbos and Pruitt (1992) and Singh and Russell (1981), respectively. Daily crop water requirement was calculated using the methods described by Doorenbos and Pruitt (1992) as described below:

$$ET_{\text{crop}} = k_c \times ET_o$$

where ET_{crop} is the crop water requirement (mm day⁻¹), ET_o is evapotranspiration of reference crop and k_c is the coefficient of the crop at different growth stages. The crop coefficient (k_c) of the Jerusalem artichoke was not found in the literature, therefore, k_c value for sunflower was used (Monti et al., 2005; Ruttanaprasert et al., 2014).

Soil evaporation (S.E.) was calculated as (Singh and Russell, 1981):

$$S.E. = \beta \left(\frac{E_0}{t} \right)$$

where S.E. is the soil evaporation (mm), β is the light transmission coefficient measured depending on crop cover, E_0 is the evaporation from class A pan (mm day⁻¹), t is the days from the last irrigation.

However, during the imposition of the irrigation treatments, soil moisture content was monitored by gravimetric method at 7-day intervals.

2.4. Data collection

The weather conditions for both years were recorded. Humidity, evaporation (E_0), and maximum and minimum temperatures were recorded daily from the time of transplanting until the harvest time using a weather station located 100 m from the experimental field.

Soil moisture contents were measured using the gravimetric method at 30, 60 and 90 DAT. The soil type at the experimental site was a loamy sand, and soil chemical and physical properties were also determined using standard laboratory methods.

In each experimental unit, relative water content (RWC) was measured at 30, 60 and 90 DAT to estimate plant water status. RWC was measured following Kramer (1980), using the second leaf from the top of the main stem and five plants for each experimental unit. The leaf was bored by a disc borer with 1 cm² in leaf area. Leaf fresh weight was measured immediately in the laboratory. Saturated weight was determined by putting the leaf sample in water for 8 h, blot drying the outer surface, and then measuring leaf saturated weight. The leaf samples were then oven-dried at 80 °C for at least 72 h or until the leaf weights were constant, and leaf dry weight was recorded. RWC was calculated using the following equation:

$$RWC = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Saturated weight} - \text{Dry weight}} \times 100$$

Two pots from each experimental unit were harvested at maturity. The matured plants determined by stem browning of 50% were cut at the soil surface and separated into leaves, stems, tubers and roots. The tubers and roots were washed in tap water to remove soil. The samples were oven-dried at 80 °C for at least 72 h or until the weights were constant. Leaf dry weight, stem dry weight, tuber dry weight, and root dry weight were recorded. Total biomass including leaf dry weight, stem dry weight, tuber dry weight and root dry weight was calculated. Harvest index was calculated as the ratio of tuber dry weight divided by total biomass.

Total crop water use (WU) was calculated by the sum of irrigation applications in each pot ± the difference in soil moisture before transplanting and soil moisture at final harvest. WUE was estimated for tuber and biomass using the formula proposed by Teare et al. (1982):

$$WUE_t = \frac{\text{tuber dry weight}}{\text{Water used in evapotranspiration}} \text{ and}$$

$$WUE_b = \frac{\text{total biomass}}{\text{water used in evapotranspiration}}$$

Percentages of reduction in tuber dry weight and total biomass from drought stress were used to evaluate the sensitivities of the Jerusalem artichoke varieties to drought stress. Percentages of reduction in tuber dry weight and total biomass were calculated for each Jerusalem artichoke variety as described by Pimratch et al. (2008).

$$\text{Percentage of reduction of yield} \left[1 - \left(\frac{\text{Weight under drought}}{\text{Weight under nondrought}} \right) \right] \times 100$$

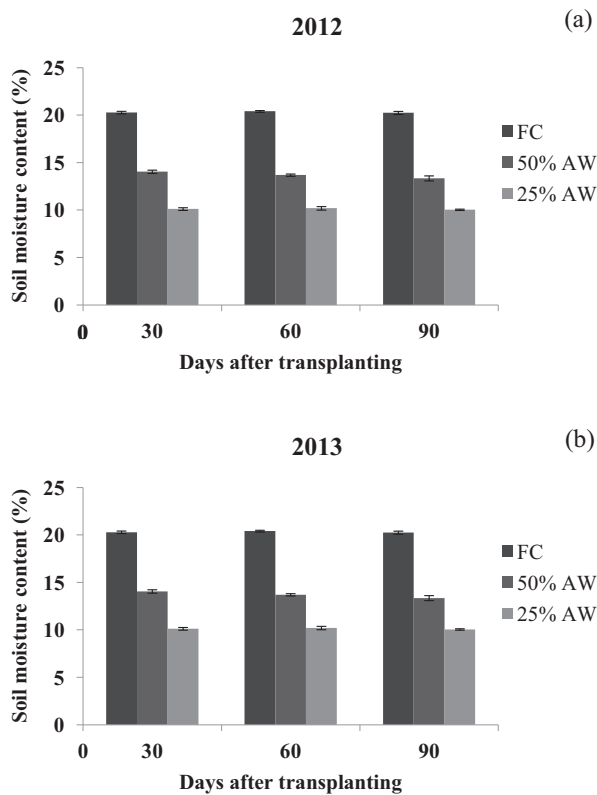


Fig. 2. Percentage of soil moisture content at 30, 60 and 90 days after transplanting in 2012 (a) and 2013 (b) (FC = field capacity, 50%AW = 50% of soil available water and 25%AW = 25% of soil available water).

2.5. Soil properties and climatic conditions

The soil used for the pot study was characterized as loamy sand soil texture with sand contents ranging from 79.93% to 81.00%, silt contents from 15.00% to 18.00% and clay contents ranging from 2.07% to 4.00%. The soil had 0.59–0.64% of organic matter, 0.02–0.03% of total nitrogen contents, 11.21–15.14 mg kg⁻¹ of phosphorus and 68.70–70.17 mg kg⁻¹ of potassium.

The meteorological data are shown in Fig. 1. Maximum temperature (T_{max}) ranged from 26.5 to 36.5 °C and minimum temperature (T_{min}) ranged from 21.3 to 26.5 °C in 2012 (Fig. 1a). In 2013, T_{max} and T_{min} ranged from 25.7 to 40.4 °C and 22.3 to 27.9 °C, respectively (Fig. 1c). Daily pan evaporations ranged from 0.3 to 7.6 mm in the first year (Fig. 1b) and 0.5 to 8.8 mm in the second year (Fig. 1d). The relative humidity values were 60–92% and 58–95% in the first and second years, respectively (Fig. 1b and d).

2.6. Soil moisture and plant water status

The differences in soil moisture contents of the three water regimes were shown among FC (well water) and the two drought stress treatments (50%AW and 25%AW) at 30, 60 and 90 DAT (Fig. 2). The results showed that the levels of drought stress were managed reasonably well.

Soil moisture contents were in accordance with the plant water status as relative water contents showed obvious differences among the three water regimes at 30, 60 and 90 DAT. The averaged soil moisture contents were 19.6–20.7%, 12.8–13.7% and 9.7–10.3% in 2012 and 20.2–20.4%, 13.3–14.0% and 10.0–10.2% in 2013 under FC, 50%AW and 25%AW, respectively (Fig. 2). The RWC values ranging from 70.3 to 91.7 were observed (Table 1). RWC values for FC treatment were significantly higher than those for 50%AW treat-

ment, whereas RWC values for 50%AW treatment were significantly higher than those for 25%AW treatment. Visual observation found that the plants grown under 50%AW showed wilting in the afternoon and the wilting symptom was more severe in the plants grown under 25%AW.

2.7. Statistical analysis

Analysis of variance was performed for each year of followed a factorial in RCBD. Homogeneity of variance was tested for all characters and combined analysis of variance of two-year data was performed (Gomez and Gomez, 1984). When the differences of main effects were significant ($P \leq 0.05$), least significant difference (LSD) was used to compare means. All calculations were performed using STATISTIX8 software program (Statistix, 2003).

The relative contribution of tuber dry weight under non-stress condition (FC) and reduction in tuber dry weight under drought stress (50%AW and 25%AW) to tuber dry weight under each drought stress condition was determined by multiple-linear regression. The analysis was based on the following statistical model (Gomez and Gomez, 1984):

$$Y_i = \alpha + \beta_1 X_{1i} + \beta_2 X_{2i} + \delta_i$$

where Y_i is tuber dry weight under drought stress of varieties i , α is the Y intercept, X_{1i} and X_{2i} are tuber dry weight under non-drought stress condition and reduction in tuber dry weight under drought stress condition of variety i , respectively, β_1 and β_2 are regression coefficients for the independent variables X_1 and X_2 , and δ_i is the associated deviation from regression.

After fitting the full model, the relative importance of the individual independent variables was determined. A sequential fit was then performed by fitting the more important variable first. The relative contributions of the individual independent variables to tuber dry weight under drought stress conditions were determined from the percentages of regression sum of squares due to the respective independent variables to total sum of squares in the sequential fitted analysis.

3. Results

3.1. Combined analysis

The effects of water (W) and variety (V) on tuber dry weight, total biomass, harvest index, WUEt and WUEb were highly significant ($P \leq 0.01$), and the interactions between water and variety ($W \times V$) were also significant for all traits (Table 2). However, year (Y) and the interaction between year and water ($Y \times W$) were significant for harvest index only. The interaction between year and variety ($Y \times V$) and the secondary levels interactions ($Y \times W \times V$) were not significantly different for all traits. However, the interactions between $W \times V$ were observed. Therefore, the data of two years were combined but performance of Jerusalem artichoke varieties were presented in separate water levels.

Water (W) contributed to a large portion of total variation for tuber dry weight (85.96%), total biomass (96.03%), harvest index (46.61%), WUEt (66.70%) and WUEb (83.93%). This revealed that water is the greatest source of variation for these traits and the management of irrigation water is an important factor for obtaining higher yields. Variety (V) had smaller effect for tuber dry weight (6.98%), total biomass (1.49%), harvest index (42.17%), WUEt (21.60%) and WUEb (4.70%). This showed that Jerusalem artichoke material in this experiment is a good source of genetic diversity for WUEt, WUEb, tuber dry weight, total biomass and especially for harvest index. Year (Y) contributed rather small portions of variation for tuber dry weight (0.04%), total biomass (0.08%), harvest

Table 1
Leaf relative water content (RWC) under three water regimes at 30 days after transplanting (DAT), 60 DAT and 90 DAT of five Jerusalem artichoke genotypes grown under three water regimes (FC = field capacity, 50%AW = 50% of soil available water and 25%AW = 25% of soil available water) in 2012 and 2013.

	RWC (%) in 2012						RWC (%) in 2013					
	30 DAT		60 DAT		90 DAT		30 DAT		60 DAT		90 DAT	
FC	88.5	a	90.9	a	91.7	a	80.2	a	85.5	a	88.7	a
50% AW	81.0	b	87.7	b	82.8	b	78.5	b	81.8	b	82.1	b
25%AW	76.9	c	84.8	c	70.3	c	75.8	c	77.7	c	76.9	c

Means in the same column followed by the same letter(s) are not different at $P \leq 0.01$ probability levels by least significant difference (LSD).

Table 2
Mean squares from combined analysis of variance for tuber dry weight, total biomass, harvest index, water use efficiency of tuber (WUEt) and water use efficiency of biomass (WUEb) of five Jerusalem artichoke varieties grown under three water regimes (FC = field capacity, 50%AW = 50% of soil available water and 25%AW = 25% of soil available water) in 2012 and 2013.

Source of variance	df	Tuber dry weight (g plant ⁻¹)	Biomass (g plant ⁻¹)	Harvest index	WUEt (g l ⁻¹)	WUEb (g l ⁻¹)
Year	1	7.45 (0.04)ns	56.60 (0.08)ns	0.0137 (0.43)**	0.0030 (0.06)ns	0.0375 (0.43)ns
Rep within year	6	2.40 (0.07)	9.80 (0.08)	0.0010 (0.18)	0.0015 (0.19)	0.0082 (0.57)
Water	2	8777.34 (85.96)**	33444.10 (96.03)**	0.7460 (46.61)**	1.5791 (66.70)**	3.6186 (83.93)**
Year × Water	2	3.82 (0.04)ns	10.20 (0.03)ns	0.0059 (0.37)*	0.0045 (0.19)ns	0.0012 (0.03)ns
Variety	4	356.23 (6.98)**	259.50 (1.49)**	0.3375 (42.17)**	0.2557 (21.60)**	0.1014 (4.70)**
Year × Variety	4	5.25 (0.10)ns	4.10 (0.02)ns	0.0023 (0.29)ns	0.0032 (0.27)ns	0.0012 (0.05)ns
Water × Variety	8	140.54 (5.51)**	114.50 (1.31)**	0.0248 (6.19)**	0.0439 (7.41)**	0.0375 (3.48)**
Year × Water × Variety	8	2.06 (0.08)ns	6.10 (0.07)ns	0.0015 (0.37)ns	0.0015 (0.26)ns	0.0043 (0.40)ns
Error	84	3.00 (1.23)	7.30 (0.88)	0.0013 (3.39)	0.0019 (3.32)	0.0066 (6.40)
Total	119					

Numbers in the parentheses are percent (%) of sum squares to total sum of squares.

ns, *, ** Non significant, significant and highly significant at $P \leq 0.05$ and ≤ 0.01 probability levels, respectively.

index (0.43%), WUEt (0.06%) and WUEb (0.43%), and the results indicated that these traits were rather consistent between years. Similarly, the interaction effects contributed small portions of variations for tuber dry weight, total biomass and harvest index, WUEt and WUEb, ranging from 0.03% to 0.37% for the interactions between year and water, ranging from 0.02% to 0.29% for interactions between year and variety and ranging from 1.31% to 7.41% for interaction between water and variety. The interaction effects, although they were significant, were lower than main effects (water and variety) for these traits.

3.2. Response of Jerusalem artichoke to the treatments

The results clearly showed that drought stress reduced tuber dry weight, total biomass, harvest index, WUEt and WUEb of the Jerusalem artichoke (Table 3). The reductions in tuber dry weight, total biomass and harvest index were more severe under severe water stress (25%AW) than mild water stress (50%AW). Overall means for tuber dry weight under FC, 50%AW and 25%AW conditions were 30.6, 10.8 and 1.6 g plant⁻¹, respectively (Table 3). On the average, drought stress at 50%AW and 25%AW reduced tuber dry weight by 64.4% and 94.9%, respectively. Significant differences among Jerusalem artichoke varieties were observed for tuber dry weight at all water regimes ($P \leq 0.01$). Tuber dry weight at FC condition ranged from 25.7 to 44.3 g plant⁻¹, at 50%AW it ranged from 4.0 to 14.7 g plant⁻¹ and at 25%AW it ranged from 0.5 to 3.0 g plant⁻¹ (Table 3). The reductions in tuber dry weight, ranging from 49.3 to 85.2% for 50%AW and 93.2 to 98.2% for 25%AW were statistically different.

Overall means for total biomass at FC, 50%AW and 25%AW conditions were 65.2, 28.9 and 8.1 g plant⁻¹, respectively (Table 3). On the average, drought stress at 50%AW and 25%AW reduced total biomass by 55.4% and 87.5%, respectively.

Overall means for harvest index were 0.47, 0.37 and 0.20 under FC, 50%AW and 25%AW, respectively (Table 3). On the average, drought stress at 50%AW and 25%AW reduced harvest index by 21.8% and 58.6%, respectively. Significant differences among

Jerusalem artichoke varieties were observed for harvest index at all water regimes ($P \leq 0.01$). Harvest index values at FC ranged from 0.39 to 0.67, at 50%AW from 0.15 to 0.52 and at 25%AW from 0.05 to 0.35.

Drought stress reduced both of WUEt and WUEb (Table 3). On the average, drought stress at 50%AW and 25%AW reduced WUEt by 29.2% and 81.3%, respectively. Drought stress at 50%AW and 25%AW reduced WUEb by 11.7% and 44.7%, respectively. Significant differences among Jerusalem artichoke varieties were observed for WUEt and WUEb at all water regimes ($P \leq 0.01$ and $P \leq 0.05$). WUEt values at FC ranged from 0.39 to 0.74 g liter⁻¹, at 50%AW from 0.13 to 0.49 g liter⁻¹ and at 25%AW from 0.03 to 0.18 g liter⁻¹. WUEb values at FC ranged from 0.88 to 1.14 g liter⁻¹, at 50%AW from 0.82 to 1.02 g liter⁻¹ and at 25%AW from 0.39 to 0.54 g liter⁻¹.

Varieties were significantly different for the reductions in tuber dry weight, total biomass and harvest index under drought conditions (Table 3). Based on reduction in tuber dry weight, Jerusalem artichoke varieties were classified into high and low groups. JA 60 and JA 125 had low reduction at 50%AW, whereas JA 5 and JA 89 had high reduction at mild water stress. At 25%AW, JA 5 had numerically the lowest reduction in tuber dry weight followed by JA 60, HEL 65, JA 125 and JA 89, respectively. However, the reductions in tuber dry weight under 25%AW for all varieties were rather high.

The varieties with low reductions in total biomass at 50%AW were HEL 65, JA 60, and JA 125, whereas JA 89 had high reduction in total biomass at 50%AW (Table 3). However, the differences in reductions in total biomass were not significant at 25%AW. At 50%AW, JA 60 had the lowest reduction in harvest index followed by JA 125, JA 5, and HEL 65. At 25%AW, JA 5 had the lowest reduction in harvest index followed by JA 60, JA 125, and HEL 65. At 50%AW and 25%AW JA 89 had the highest reduction in harvest index. The differential responses under different levels of available soil water also indicated the importance of stress levels in assessing drought resistance in Jerusalem artichoke.

There were significant genotypic differences for tuber dry weight at each level of available soil water (Table 3). JA 5 had high tuber dry weight at all water regimes but it had rather high reduc-

Table 3
Tuber dry weight, total biomass production, harvest index, the reductions in these traits, water use efficiency of tuber and water use efficiency of biomass under different water regimes for five Jerusalem artichoke varieties.

Varieties	Tuber dry weight (g plant ⁻¹)		Reduction (%)		Total biomass (g plant ⁻¹)		Reduction (%)		Harvest index		Reduction (%)		Water efficiency of tuber yield (g l ⁻¹)		Water efficiency of biomass (g l ⁻¹)						
	FC	50%AW	25%AW	50%AW	25%AW	FC	50%AW	25%AW	FC	50%AW	25%AW	50%AW	25%AW	FC	50%AW	25%AW					
JA 60	26.5c	13.3ab	1.6b	49.3c	93.9b	55.5d	26.3c	6.6c	51.1c	88.0	0.48b	0.51a	0.24b	-6.2d	49.4b	0.42bc	0.10b	0.88d	0.82c	0.39c	
JA 125	29.2b	12.4b	1.5b	57.0c	94.8b	74.1a	33.5a	7.9abc	54.8bc	89.4	0.39c	0.37b	0.18c	6.0c	52.6b	0.45b	0.38b	1.14a	1.02a	0.42bc	
JA 5	44.3a	14.7ab	3.0a	66.8b	93.2b	66.1b	27.8bc	8.6ab	58.0ab	87.0	0.67a	0.52a	0.35a	21.7b	47.8b	0.74a	0.49a	1.10ab	0.93b	0.50ab	
JA 89	27.2bc	4.0d	0.5c	85.2a	98.2a	69.2b	27.0c	9.7a	60.8a	85.8	0.40c	0.15d	0.05d	62.2a	86.8a	0.42bc	0.13d	1.06b	0.84c	0.54a	
HEL 65	25.7c	9.3c	1.4b	63.6bc	94.6b	61.2c	30.0b	7.7bc	51.0c	87.4	0.42c	0.31c	0.18c	25.4b	56.6b	0.39c	0.29c	0.94c	0.93b	0.43bc	
Means	30.6	10.8	1.6	64.4	94.9	65.2	28.9	8.1	55.4	87.5	0.5	0.4	0.2	21.8	58.6	0.48	0.34	1.03	0.91	0.46	
F-test	**	**	**	**	**	**	**	*	**	ns	**	**	**	**	**	**	**	**	**	**	*

Means in the same column followed by the same letter (s) are not different at $P \leq 0.05$ probability levels by least significant difference (LSD).

FC = field capacity, 50%AW = 50% of soil available water and 25% = 25% of soil available water.

ns, *, **, Non significant, significant and highly significant at $P \leq 0.05$ and ≤ 0.01 probability levels, respectively.

tions in tuber dry weight at 50%AW and 25%AW. JA 60 and JA 125 had rather low tuber dry weight at FC but they had high tuber dry weight at 50%AW and rather low tuber dry weight at 25%AW. However, JA 60 and JA 125 had low reduction in tuber dry weight at 50%AW. Conversely, JA 89 and HEL 65 had low tuber dry weight at all of water regimes. The reduction in tuber dry weight of JA 89 and HEL 65 were high under both 50%AW and 25%AW.

Jerusalem artichoke varieties responded differently for total biomass (Table 3). JA 125, JA 89 and JA 5 had high total biomass at FC and 25%AW, and the reduction in total biomass at 50%AW and 25%AW was also high in these varieties. JA 60 had low total biomass at all of water regimes and it had low reduction of total biomass at 50%AW. HEL 65 had low total biomass at FC and 25%AW but it had relatively high total biomass at 50%AW. Low reduction in total biomass was observed in HEL 65 at 50%AW. The reductions in total biomass were high and the differences in the reduction in total biomass at 25%AW were not significant among Jerusalem artichoke varieties.

Significant differences among Jerusalem artichoke varieties were observed for harvest index at all water regimes (Table 3). JA 5 had the highest harvest index at all water regimes but the reduction in harvest index for JA 5 was low at 50%AW and 25%AW. JA 60 and JA 125 had relatively low harvest index at FC but had high harvest index at 50%AW. JA 60 and JA 125 had low reduction in harvest index at 50%AW and 25%AW. JA 89 had low harvest index at all water regimes and also had high reductions in harvest index at 50%AW and 25%AW. HEL 65 had low harvest index at all water regimes. At 25%AW, JA 5 also had the highest tuber dry weight, and it also had the highest harvest index at all water regimes.

Significant differences among Jerusalem artichoke varieties were observed for WUEt at all water regimes (Table 3). JA 5 had the highest WUEt at all water regimes. HEL 65 had the lowest WUEt at FC. Under 50%AW condition, JA 89 and HEL 65 had rather low WUEt. However, all of JA varieties had very low WUEt when compare with well watered conditions (FC). The same trend in WUEb under FC showed that JA 125 and JA 5 had high WUEb. JA 125, JA 5 and HEL 65 had high WUEb under 50%AW. The results revealed that JA 5 is the best variety in this study because it had the highest tuber dry weight, harvest index, WUEt and WUEb under both well watered conditions and drought stress conditions.

3.3. Factors contributing to tuber dry weight, total biomass production and harvest index under drought stress

Regression analysis explained 98.4% and 98.7% of the total variations in tuber yield at 50%AW and 25%AW, respectively (Table 4). At 50%AW, yield reduction contributed a larger portion of total variation (64.8%), whereas yield potential at FC contributed a smaller portion of total variation (33.6%). At 25%AW, yield reduction still contributed a larger portion of total variation (76.5%), whereas yield potential at FC contributed a smaller portion (22.2%).

Regression analysis also showed that the contribution of total biomass under FC and the reduction in total biomass at 50%AW were 79.2% and 19.8% respectively (Table 4). The relative contributions of these factors were not significant at 25%AW in which the contribution of total biomass at FC and the reduction in total biomass at 25%AW were 9.1% and 1.4%, respectively. In addition, the regression analysis confirmed that 99.3% and 98.9% of total variations in harvest index was at 50%AW and 25%AW, respectively (Table 4). At 50%AW, yield reduction contributed a larger portion of total variation (66.0%), whereas yield potential at FC contributed a smaller portion of total variation (33.4%). At 25%AW, yield reduction still contributed a larger portion of total variation (76.1%), whereas yield potential at FC contributed a smaller portion (22.8%). The results indicated that low yield reduction in tuber yield under drought was more important than high yield potential under FC.

Table 4
Contribution of potential of tuber dry weight, total biomass and harvest index at field capacity and the reduction of tuber dry weight, total biomass and harvest index to tuber dry weight, total biomass and harvest index under drought stress (50%AW and 25%AW).

	Tuber dry weight		Total biomass		Harvest index	
	Explained by regression (%)		Explained by regression (%)		Explained by regression (%)	
At 50%AW						
Regression	98.4	**	99.0	**	99.3	**
Reduction in tuber yield at 50%AW	64.8	**	79.2	**	66.0	**
Potential of tuber yield at FC	33.6	**	19.8	**	33.4	**
At 25%AW						
Regression	98.7	**	10.5	*	98.9	**
Reduction in tuber yield at 25%AW	76.5	**	9.1	ns	76.1	**
Potential of tuber yield at FC	22.2	**	1.4	ns	22.8	**

FC, Field capacity; AW, available soil water.

ns, *,** Non significant, significant and highly significant at $P \leq 0.05$ and ≤ 0.01 probability levels, respectively.

The overall results of this study indicated that low yield reduction in tuber yield, total biomass and harvest index under drought was more important than high yield potential under FC.

4. Discussion

Several studies were conducted to determine the effects of water stress on tuber yield and biomass of Jerusalem artichoke in both temperate (Conde et al., 1991; Losavio et al., 1997; Schittenhelm, 1999; Monti et al., 2005; Liu et al., 2012) and tropic regions (Ruttanaprasert et al., 2014). However, these previous studies did not focus on determining the effects of soil moisture content on tuber dry weight and total biomass (including root mass) of Jerusalem artichoke with different levels of drought resistance. Therefore, this study was undertaken to compare the responses to various soil moisture levels on Jerusalem artichoke varieties varying in drought resistance levels. The management of irrigation water for growing Jerusalem artichoke in the pot experiment permitted more precise control of water supplied to each of the treatments in comparison to if the same experiment would have been conducted in the field.

In this study, drought reduced tuber dry weight and biomass, and the reductions in tuber dry weight and biomass were greater under severe drought (85.8–98.2%) in comparison to moderate drought (49.3–85.2%) conditions. The results of this study clearly indicated that Jerusalem artichoke in general is not a drought resistant crop as biomass was reduced greatly especially in the tropics even under mild drought stress. In temperate region, drought stress reduced tuber dry weight of 20% (Conde et al., 1991; Losavio et al., 1997). Loss of tuber yield of more than 29% in tropical regions with high temperature was observed (Ruttanaprasert et al., 2014). Yield loss in this study was much higher than that reported previously under drought during the dry period with low temperature and short photoperiod in tropical area (Ruttanaprasert et al., 2013; Ruttanaprasert et al., 2014) and temperate regions (Conde et al., 1991; Losavio et al., 1997). Lower reduction in yields in the temperate regions was possibly due to lower temperature (12.7–24.2 °C) (Conde et al., 1991) as drought in the tropics during the rainy season is usually associated with high temperatures (18.4–30.5 °C) (Ruttanaprasert et al., 2014). High temperatures promote vegetative growth rather than partition of assimilates into harvestable tubers (Ruttanaprasert et al., 2013). In addition, low temperature conditions result in low evaporation demands, therefore, water deficits develop slower in the plants (Denmead and Shaw, 1962).

Drought stress reduced harvest index of Jerusalem artichoke from 0.47 to 0.20 in this study. Similarly, harvest index of potato was reduced by terminal drought stress from 0.35 to 0.30 (Schafleitner et al., 2007). It is our general understanding that drought reduces growth and yield component traits in most crops

species. However, drought can increase harvest index in some cases. In a previous study on Jerusalem artichoke, drought stress increased harvest index from 0.60 to 0.73 (Conde et al., 1991). However, the increase in harvest index as affected by drought was not high compared to the reduction in yield. Jefferies (1992) found that long term drought stress increased harvest index of potato in some early maturity varieties (from 0.41 to 0.50) but reduced one late maturity variety (from 0.54 to 0.25). Long term drought provides enough time for the crop for acclimatization or adaptation to gradual soil drying (Chaves et al., 2003). Brief and severe drought events, especially late in the growing season, severely reduces harvest index (Jefferies, 1995).

The results this study has clearly indicated that drought has large effects on harvest index. These differences in response may reflect variety differences in development and also differences in the severity of the water stress. Therefore, the more severe drought stress may decrease harvest index. The reasons for this difference in responses are not obvious and further work will be necessary both to confirm the difference and to clarify the basis of the difference.

The means for harvest index in this study were lower than the harvest index in the previous study. Harvest indices of Jerusalem artichoke were 0.60 under well water condition, 0.72 under water stress and 0.73 under severe drought stress Conde et al. (1991). More severe drought stress and higher temperatures in our study might be the causes of the lower harvest index. Nevertheless, harvest index of a tuber crop is an important trait determining yield under drought conditions (Deguchi et al., 2010). Therefore, improvement of Jerusalem artichoke with high tuber yield and harvest index is an important objective in Jerusalem artichoke drought tolerant breeding programs. The results of this study revealed that JA 5 had high harvest index both under well watered and water stress conditions.

Drought stress reduced WUEt and WUEb in this study. Janket et al. (2013) found that mild water stress reduced WUEt and WUEb by 2.4–9.9% and 3.2–7.1%, respectively. On the other hand, under severe water stress drought increased WUEt and WUEb by 4.0–5.2% and 3.8–4.9%, respectively. Conde et al. (1997) also found that drought stress by applying the 50%ET of irrigation increased WUEt from 1.4 to 1.9 g liter⁻¹ or 35.7%. The reasons for this difference may be because of differences in the levels of water stress, and differences in air temperature.

The ranges of WUEt were 0.03–0.74 g liter⁻¹. The previous report in temperate regions showed WUEt as high as 1.1–1.9 g liter⁻¹ (Conde et al., 1991). The differences in the results from distinct studies are due to difference in plant material, weather condition, times of drought imposition to the crops and drought intensity.

The differences in tuber dry weight, total biomass, WUEt and WUEb and harvest index indicated genetic variability in these tested materials. In general, the variety with high tuber dry weight,

total biomass, and harvest index at FC also had high tuber dry weight at 50%AW and to a lesser extent at 25%AW.

JA 89 and HEL 65 were defined as the varieties with high tuber yield under drought stress in Ruttanaprasert et al. (2014). However, they were classified in the group with the lowest tuber yield under drought stress in this study. Difference in crop performance in different studies could be due to difference in weather conditions especially temperature and photoperiod. It is possible that JA 89 and HEL 65 were more sensitive to high temperature and long photoperiod (Ruttanaprasert et al., 2013). JA 5 had medium tuber yield under drought stress in the dry period and it showed highest tuber yield in this study. This suggested that JA 5 was a variety with stable yield in response to drought stress.

Most Jerusalem artichoke varieties in this study had low tuber dry weight and also high percent reduction in tuber dry weight except for JA 5, which had the highest tuber yield under both, well watered and drought stress conditions. However, the ideal variety with high yield potential and low yield reduction under drought stress was not found in our experiment. Therefore, selection and breeding for high yield potential varieties under well-watered conditions and low reduction under drought stress should be investigated in further research.

5. Conclusions

This study resulted in the following key conclusions:

- 1) Drought reduced tuber dry weight, total biomass, harvest index, WUEt, WUEb, and the reductions were more severe at the highest level of water stress (25%AW) imposed in this study compared to the mild water stress level (50%AW). Differences among Jerusalem artichoke varieties were significant for tuber dry weight, total biomass, harvest index, WUEt and WUEb at all water regimes. Variations in high tuber dry weight, total biomass and harvest index were higher at 50%AW than at 25%AW, and selection for superior varieties for these traits should be carried out at 50%AW.
- 2) Jerusalem artichoke varieties could be classified into three groups based on the responses to drought for tuber dry weight. The variety JA 5 was classified as the variety with high yield potential and high yield reduction, group 2 consisted of JA 60 and JA 125 with low yield potential and low yield reduction, and group 3 included JA 89 and HEL 65 with low yield potential and high yield reduction.
- 3) Tuber yield, total biomass and harvest index at 50%AW and 25%AW depended largely on the reductions of tuber yield, total biomass and harvest index under drought and, to less extent, tuber yield potential under well-watered conditions (FC). The development of Jerusalem artichoke varieties with low reduction of productivity under drought stress should enhance tuber yield, total biomass and harvest index.

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